Evolutionary Models: Movement and Mixing in Trait and Physical Space

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Over generations, a species will evolve to increase its fitness to its environment. Natural selection is the primary mechanism by which this occurs, wherein environmental pressures cause individuals with more fit phenotypes to reproduce at a higher rate. For the purpose of modeling, the space of possible heritable traits may be viewed as a continuum, and a particular individual as inhabiting a point in trait space. Making the biomass continuous as well, a population is viewed as a distribution in trait space. In this view, natural selection is the process by which the distribution of biomass propagates through trait space, generally increasing its average fitness.

1 Building blocks for models

The first step in modeling a system in which the dominant traits can change is defining a suitable measure of how much of a species there is. While the actual number of members of the species is an option, a more useful measure is the biomass, b, which readily translates across species. The biomass density can be treated as a function over space, time, and this "trait-space"

$$b(\mathbf{x}, t | s_1, s_2, ...)$$

where the variables $\mathbf{s} = \{s_1, s_2, \ldots\}$ specify the phenotype, or traits, of the organism. In addition to the biomass, the rates of survival and reproduction depend on the environmental conditions and vary with phenotype. These rates are defined as

$$\mathcal{R} = \mathcal{R}(\mathbf{s}|E) \quad , \quad \mathcal{R}(\mathbf{s}_1|E) \neq \mathcal{R}(\mathbf{s}_2|E)$$

where E represents the environmental conditions. The biomass evolution is related to the growth rate (including reproduction) by

$$\frac{\partial}{\partial t} b(\mathbf{s}) = \mathcal{R}(\mathbf{s}|E) b(\mathbf{s}) \ldots \tag{1}$$

indicating that new organisms (represented as biomass) have the same values of $\mathbf{s}$ as their parents. However, in nature genetic mutation can occur causing the offspring of parents to have a slightly different trait values. (And, since these represent phenotypes, there is some degree of natural variation as well.) This can be modeled by changing Equation 1 to

$$\frac{\partial}{\partial t} b(s) = \mathcal{R}(\mathbf{s}|E) b(\mathbf{s}) + \nabla_s^2 mb \tag{2}$$

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14. ABSTRACT
Over generations, a species will evolve to increase its fitness to its environment. Natural selection is the primary mechanism by which this occurs, wherein environmental pressures cause individuals with more fit phenotypes to reproduce at a higher rate. For the purpose of modeling, the space of possible heritable traits may be viewed as a continuum, and a particular individual as inhabiting a point in trait space. Making the biomass continuous as well, a population is viewed as a distribution in trait space. In this view, natural selection is the process by which the distribution of biomass propagates through trait space, generally increasing its average fitness.

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where m is a type of trait diffusion (which can be proportional to the reproduction rate). The rate appears within the derivatives for the same reasons it does in the Fokker-Planck equation (or the representation of kinesis in a previous lecture) – the length of the random jump in trait space is set at the beginning of the excursion (and there is no reason to expect non-divergence). In any case, we shall just use the over-simplification of treating m as constant.

The simplified model created in Equation 2 obviously has a number of flaws. If a trait is not represented in the initial modeling it will never arise long term meaning that a full trait space needs to be known *a priori*. Additionally, the time scales are not well-defined. While there is some idea of the rate of genetic changes, not much about how this translates into alterations of the phenotype is understood. Finally, since natural selection acts on an individual basis; a model based on biomass may not accurately model the dynamics for low values where extinction is probable.

If we extend the above model to start accounting for advection and diffusion in space as well as diffusion in trait space, we can use the following equation to model a wide variety of systems

$$\frac{D}{Dt}b - \nabla\kappa\nabla b = b\mathcal{R}(\mathbf{s}|E) + \nabla_s^2 mb.$$

With this governing equation the following topics will be examined

- Evolutionarily stable strategies: what s values are selected for?

- Relationship to stability theory

- Adaptive dynamics in the presence of mutation

- Effects of mixing, diffusion, and advection

2   A Simple Model

To make a model which can be studied easily, it is necessary to create a function for the growth rate. For a first model, we make a number of simplifying assumptions: the organisms will have a 1D trait space, $\mathbf{s} = s$, and use a common resource, N, so that the amount available per individual is

$$N_I = N\frac{b_0}{\int ds\ b(s)}$$

where b_0 corresponds to the biomass of a single individual and the notation $\langle b \rangle = \int ds\ b$ has been used. Growth will occur when $N_I > N_{crit}$ but saturates to a maximum value g_m when the resources are plentiful. For example,

$$g = g_m\frac{N_I - N_{crit}}{N_I} \text{ for } N_I > N_{crit},$$

which results in a logistic-like system:

$$\frac{\partial}{\partial t}b = \left[g_m\left(1 - \frac{\langle b \rangle}{b_c}\right) - d \right]b + m\frac{\partial^2}{\partial s^2}b \tag{3}$$

The coefficients g_m (maximum growth rate), d (death rate), and $b_c = Nb_0/N_{crit}$ (carrying capacity) are functions of s. For this form,

$$\mathcal{R}(s|E) = \mathcal{R}(s|\langle b\rangle) = g_m\left(1 - \frac{\langle b\rangle}{b_c}\right) - d.$$

The environment here is the density of competitors for the resource as well as the value of N implicit in the carrying capacity b_c.

3   Evolutionarily Stable Strategies (ESS)

If the system modeled by Equation 3 is analyzed without considering mutation ($m = 0$), there are many possible singular solutions of the form

$$b(s,t) = \bar{b}(t)\delta(s - \bar{s})$$

with $\bar{b}$ satisfying

$$\frac{\partial}{\partial t}\bar{b} = \mathcal{R}(\bar{s}|\bar{b})\bar{b}$$

since $E = \langle b\rangle = \bar{b}$. This results in just the logistic equation and steady solutions where $\mathcal{R}(\bar{s}|\bar{b}) = 0$ indicating

$$\bar{b} \to b_c(\bar{s})\left(1 - \frac{d(\bar{s})}{g_m(\bar{s})}\right)$$

Let us introduce a different organism with phenotype s': $b = \bar{b}(t)\delta(s - \bar{s}) + b'(t)\delta(s - s')$; if its biomass is very low when compared to $\bar{b}$, Equation 3 becomes

$$\frac{1}{b'}\frac{\partial}{\partial t}b' = \mathcal{R}(s'|\bar{b}) = \left[g_m(s')\left(1 - \frac{\bar{b}}{b_c(s')}\right) - d(s')\right],$$

and when the coefficients are time-independent, we can write this in the simpler form

$$\frac{1}{b'}\frac{\partial}{\partial t}b' = g_m(s')\frac{\bar{b}(s') - \bar{b}(\bar{s})}{b_c(s')}$$

where $\bar{b}(s')$ is the equilibrium population for $s = s'$. For this model, the population with the highest equilibrium value will exclude all others: b' will decay if $\bar{b}(s') < \bar{b}(\bar{s})$. Alternatively, the ESS maximizes $b_c(s)[g_m(s) - d(s)]/g_m(s)$, and it's also the one which can survive on the minimum resource N_I.

In other situations, there may be no single species which can out-compete all others. For example, consider a case in which different species use somewhat different resources so that N_I for a species s depends on the nearby biomass but not species far away in trait space. E.g, is s represents the size of a herbivore, it will generally feed on a limited range of plant sizes. This kind of local competition could look like

$$\mathcal{R} = g_m\left[1 - \int ds'w(s|s')b(s')\right] - d$$

with w a peaked function. Since we will take b_c to be constant, we can just choose it to be one hereafter; w will be normalized to have unit integral. Figure 1 shows an example with speciation events and a final state with 6 "species."
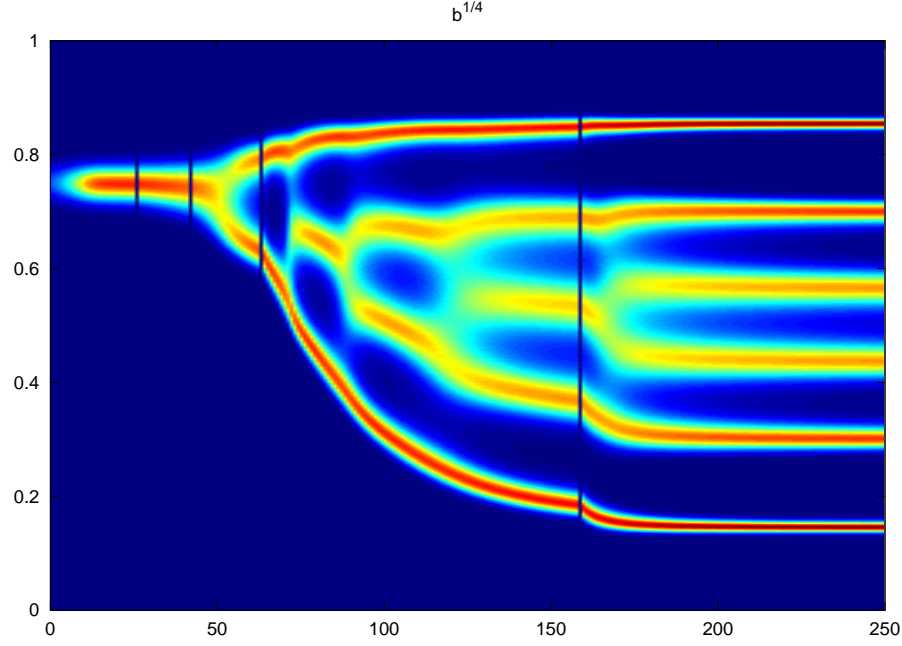
$b^{1/4}$

Figure 1: Biomass density vs. time for the case of local competition. The y axis is s; the x axis is time, but on an uneven scale. The black lines show where the time scale changes from 1 day per unit to 5, 10, 50, and 500 days.

4 Adaptive dynamics

Dieckmann points out that the dynamics may be approximated by equations for the net population and the rate of movement in trait space.

We can look at the (local) mean biomass and the mean value of s

$$\langle b \rangle = \int_{s_0}^{s_1} ds\, b(s)$$

$$\langle s \rangle = \langle sb \rangle / \langle b \rangle$$

Applying the local average to a system defined in Equation 2 and ignoring fluxes out of the range by mutation, we get

$$\frac{\partial}{\partial t} \langle b \rangle = \langle \mathcal{R}(s, b) b \rangle$$

which is

$$\simeq \mathcal{R}(\langle s \rangle, \tilde{b}) \langle b \rangle + \frac{1}{2} \mathcal{R}'' \sigma^2 \langle b \rangle$$

from Taylor expansion. For evaluating the competition/ environmental effects, we can treat the biomass distribution as a set of singular values

$$\tilde{b} = \langle b \rangle_i \delta(s - \langle s \rangle_i)$$

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Taking the local s moment and expanding gives

$$\frac{\partial}{\partial t}\langle s\rangle\langle b\rangle = \langle s\mathcal{R}b\rangle$$

$$\langle b\rangle\frac{\partial}{\partial t}\langle s\rangle = \langle(s - \langle s\rangle)\mathcal{R}b\rangle$$

$$\simeq \mathcal{R}'\sigma^2\langle b\rangle$$

$$\frac{\partial}{\partial t}\langle s\rangle \simeq \mathcal{R}'\sigma^2$$

The speed at which the peaks migrate towards the optimal value depends on the gradient and on the width of the distribution σ. Spread arises from mutation or from migration mixing. We could derive an equation for σ; it tends to increase because of m and decrease because of negative curvature in $\mathcal{R}$ which acts to sharpen peaks.

As a simple, and analytically tractable example for a single peak, consider a system with

$$\mathcal{R} = \left[R_0 - \frac{1}{2}R_2(s - s_0)^2\right]\left[1 - \frac{1}{\sqrt{2\pi}}\langle b\rangle\right]$$

where R_0, R_2, and s_0 could be functions of time as the population or other processes alter the resource. We can find a time-dependent solution (without needing to approximate)

$$b = b_0(t)\exp\left[-\frac{1}{2}\frac{[s - x(t)]^2}{\sigma^2(t)}\right]$$

when

$$rcl\frac{\partial}{\partial t}\sigma = -\frac{1}{2}R_2^*\sigma^3 + \frac{m}{\sigma}$$

$$\frac{\partial}{\partial t}x = -R_2^*\sigma^2(x - s_0)$$

$$\frac{1}{b_0}\frac{\partial}{\partial t}b_0 = R_0^* - \frac{1}{2}R_2^*(x - s_0)^2 - \frac{m}{\sigma^2}$$

with $R_j^* = R_j(1 - \sigma b_0)$.

The center of the distribution moves towards the peak in the growth rate curve at a speed which depends of the slope at the current center location $[-R_2^*(x - s_0)]$ and the variance of the distribution. The width asymptotes to the value $(2m/R_2^*)^{1/4}$ (if $\mathcal{R}''$ is negative) which narrows as the growth rate curve becomes more sharply peaked. The population will increase or decrease depending on the sign of $R_0^* - m/\sigma^2$; the dynamics of the resource will adjust R_0^* until it reaches the equilibrium value.

The environment will be time-dependent because of many external factors, so that $\mathcal{R}$ itself has a whole spectrum of variability. The velocity for movement in trait space will therefore be fluctuating, and we cannot expect the system to be in equilibrium. If the

external changes are very slow compared to mutation times, the system will be very close to the ESS for current conditions:

$$\frac{\partial \mathcal{R}(\mathbf{s},t)}{\partial s_i}\bigg|_{\mathbf{s}=\bar{\mathbf{s}}(t)} \simeq 0$$

In contrast, if the environmental fluctuations are fast, the center of the distribution will not be able to keep up, and the mean trait value will settle at the point where the time-averaged velocity is zero

$$\left\langle \frac{\partial \mathcal{R}(\mathbf{s},t)}{\partial s_i}\bigg|_{\mathbf{s}=\bar{\mathbf{s}}} \right\rangle \simeq 0$$

For intermediate time-scales, comparable to mutation times, the center of the distribution will partially, but not completely, track the variations. The population dynamics is implicit here, basically maintaining $\mathcal{R}(\bar{s},t)$; as we shall see, it may play a much more active role with multiple trophic levels.

5 Time-dependent

We can also consider a system distributed in trait- and physical space in which a changing environment produces time-dependent forcing. A simple way to do this is to change the reproduction rate in such a way that favors different phenotypes at different times. This could model such changing environmental parameters as mixed layer depth, or sunlight, for example. During the portion of the forcing cycle when a certain phenotype is not fit, mutation can replenish such populations which would otherwise slowly die out. We can then see a seasonal cycle in the community structure as well as the biomass. Alternatively, selective grazing in which the zooplankton feed more heavily on the more abundant species can also prevent the non-optimal species from disappearing.

If the growth rate is time-dependent, $\frac{\partial}{\partial t}\mathcal{R} \neq 0$, a time-average of the biomass can be taken to find

$$\frac{1}{T}\ln\frac{b'(T)}{b'(0)} = \langle \mathcal{R}(s',t|\bar{b}(\bar{s},t))\rangle \equiv R(s'|\bar{s})$$

Then, based on this result, $\bar{s}$ will represent an evolutionarily stable strategy if

$$R(\bar{s}|\bar{s}) = 0 \quad \text{[definition]} \qquad \text{and} \qquad R(s'|\bar{s}) < 0 \quad \text{for} \ \ s' \neq \bar{s}$$

which indicates that organisms with a non-optimal phenotype will die out representing natural selection. Locally, these conditions become

$$\frac{\partial}{\partial s'}R(s'|\bar{s})\big|_{s'=\bar{s}} = 0 \quad , \qquad \frac{\partial^2}{\partial s'^2}R(s'|\bar{s})\big|_{s'=\bar{s}} < 0,$$

but since the competition is temporally local, it is possible that several species could coexist with one or another dominant at different times.
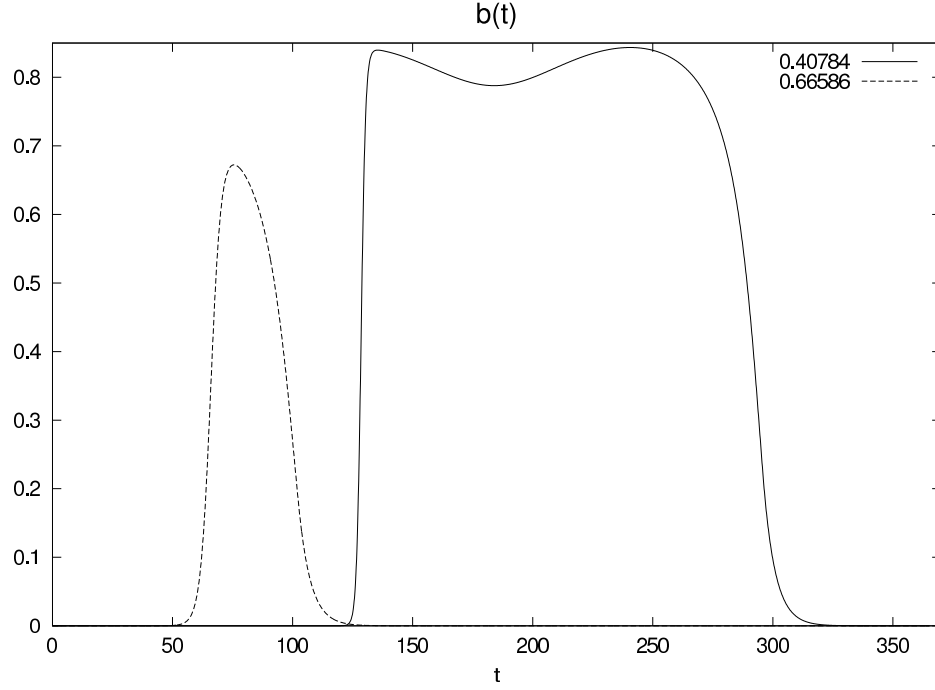
Figure 2: Biomass density vs. time for $s = 0.41$ (late) and for the case of local competition. The y axis is s; the x axis is time, but on an uneven scale. The black lines show where the time scale changes from 1 day per unit to 5, 10, 50, and 500 days.

6 Relationship to stability theory

To understand the relationship to stability theory, look again at the linearized model

$$\frac{\partial}{\partial t}b' = \mathcal{R}(s|\bar{b})b' + \bar{b}\frac{\partial \mathcal{R}}{\partial E}\langle b'\rangle$$

with the basic state having

$$\bar{b}(s)\mathcal{R}(s|\bar{b}(s)) = 0$$

- Standard problems: $\bar{b}(s) \neq 0 \Rightarrow \mathcal{R}(s, \bar{b}(s)) = 0$, the first term vanishes, and we deal with the second term, often in the form

$$\frac{\partial}{\partial t}b'_i = \bar{b}_i\frac{\partial \mathcal{R}_i}{\partial b_j}\bigg|_{b=\bar{b}}b'_j$$

- Evolutionarily Stable Strategies: $\bar{b}(s) = 0$ for $s \neq \bar{s}$ so that $\mathcal{R}(s|\bar{b}) \neq 0$ and the first term is the important one.

In the case with mutation

$$\bar{b}\mathcal{R}(s|\bar{b}) + \nabla_s^2 m\,\bar{b} = 0$$

$$\frac{\partial}{\partial t}b' = \mathcal{R}(s|\bar{b})b' + \bar{b}\frac{\partial \mathcal{R}}{\partial E}\langle b'\rangle + \nabla_s^2 m\,b'$$

both terms enter. Near the "hot-spots" where $\bar{b}$ is large, $\mathcal{R}$ is relatively small, the second term dominates and the problem looks like a standard stability system modified by diffusion. Far away, however, $\bar{b}$ is small, and the basic state has a decaying form with $\mathcal{R}$ nonzero. If $\mathcal{R}$ changes and becomes positive in that region, the population can "tunnel" into the local maximum and grow. The amount of time this will take depends on distance and the mutation rate.

7 Physical mixing

We now consider a model with a single spacial dimension, y, in addition to the single phenotype dimension, s. Our growth rate varies in physical space, and the biomass also diffuses in physical space, but we neglect the diffusion in trait space that represents mutation.

$$\frac{\partial}{\partial t}b = b\mathcal{R}(s, y | \langle b \rangle) + \kappa \frac{\partial^2}{\partial y^2}b,$$

with

$$\mathcal{R} = \left[R_0 - \tfrac{1}{2}R_2(s - s_0(y))^2 \right]\left[1 - \langle b \rangle \right] - d.$$

Figure 3 shows the biomass concentrates into a limited number of species occupying overlapping latitude ranges; intermediate species are excluded.
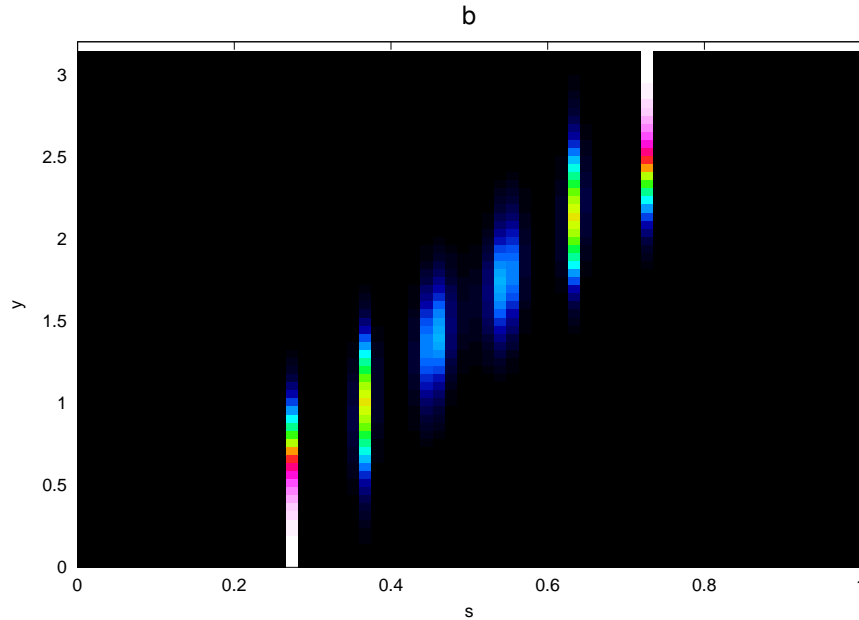

Figure 3: Biomass density $b(s)$ vs. y (non-dimensional) with physical mixing.

Because there is no mutation, we can analyze this behavior by examining singular solutions with the single-phenotype ansatz,

$$b(s, y, t) = \bar{b}(y, t)\delta(s - \bar{s}).$$

Applying this ansatz yields the PDE in y and t that governs $\bar{b}$,

$$\frac{\partial}{\partial t}\bar{b} = \left(\left[R_0 - \tfrac{1}{2}R_2(\bar{s} - s_0(y))^2\right]\left[1 - \bar{b}\right] - d\right)\bar{b} + \kappa\frac{\partial^2}{\partial y^2}\bar{b}.$$

Note that the linear part of this operator is a Schrödinger equation,

$$\frac{\partial}{\partial t}\bar{b} = r(y)\bar{b} + \kappa\frac{\partial^2}{\partial y^2}\bar{b},$$

which has a trapped mode if the region where $\mathcal{R}(\bar{s}, y|0) > 0$ is big enough and strong enough to overcome diffusive losses into the region where the death rate dominates (Kierstead and Slobodkin).

To determine whether a steady single-phenotype solution is linearly stable to nearby species (i.e. is a local ESS), consider small perturbations, $b(s, y, t) = \bar{b}(y) + b'(\bar{s} + s', y, t)$. To linear order in s' and b', the perturbations are governed by

$$\frac{\partial}{\partial t}b' = b'\mathcal{R}(\bar{s}, y, \bar{b}) + s'\bar{b}\frac{\partial\mathcal{R}}{\partial s}(\bar{s}, y, \bar{b}) + \kappa\frac{\partial^2}{\partial y^2}b'.$$

If $\bar{s}$ is a local ESS, the growth rate for b' will be zero, and we would need one higher order is s' to decide if the state is a local minimum or maximum. Thus, we want to find the $\bar{s}$ such that

$$0 = b'\mathcal{R}(\bar{s}, y, \bar{b}) + s'\bar{b}\frac{\partial\mathcal{R}}{\partial s}(\bar{s}, y, \bar{b}) + \kappa\frac{\partial^2}{\partial y^2}b'.$$

in the limit as $s' \to 0$. Multiplying this equation by $\bar{b}$ and the equation for the latter by b' and integrating over space implies

$$\int d\mathbf{x}\,\bar{b}\,b'\frac{\partial\mathcal{R}}{\partial s}(\bar{s}, y, \bar{b}) = 0$$

In the limit, $b' \to \bar{b}$, so we can pick an $\bar{s}$, find $\bar{b}$, evaluate this integral, and search for the $\bar{s}$ where it vanishes. Species near this value will be excluded; however, the growth rate for ones far away, found from

$$\sigma b' = \mathcal{R}(s, y, \bar{b})b' + \kappa\frac{\partial^2}{\partial y^2}b',$$

may be positive. In that case, another band will appear. This can happen because $\bar{b}$ varies spatially, so it is not effective at excluding others in the regions where $\bar{b}$ is small and is dying out but sustained by diffusion from the positive growth regions.

Simulations of this spatial-diffusion model give the following qualitative results:

- The single species solution has reduced amplitude and will die out if κ is big and the volume average of $\mathcal{R}(s|0)$ is negative.

- If $b(\bar{s}, y)$ is large enough, single solutions may damp the rest of the field, even when it would otherwise grow.

- Discrete species with different phenotypes emerge in spatially-separated bands.

8 Predator-prey

We now present a model with a predator species (zooplankton, Z) and a prey species (phytoplankton, P) evolving in a one-dimensional trait space. The prey has a trait-dependent birth rate, the predator has a constant death rate, and the predator feeds on the prey according to their respective traits, as governed by the interaction kernel, G.

$$\frac{D}{Dt}P(s) = \left[\mu(s)N - \int ds' \, G(s - s')Z(s') \right] P$$

$$\frac{D}{Dt}Z(s') = \left[a \int ds \, G(s - s')P(s) - d_z \right] Z,$$

with μ peaked at $s = 0$ and $G(s - s')$ peaked at zero. We also require that the total biomass be preserved:

$$N + \int ds \, P(s) + \int ds' \, Z(s').$$

This system has a singular solution,

$$(P, Z) = (\bar{P}\delta(s), \bar{Z}\delta(s')),$$

which is an ESS, but it may be unstable if

$$|G''(0)|\bar{Z} > |\mu''(0)|\bar{N}.$$

or if

$$\frac{|G''(0)|}{G(0)} > \frac{|\mu''(0)|}{\mu(0)},$$

so that the predation function is sharply curved and inhibits growth only in a small neighborhood of the single-phenotype solutions. The figures show two examples of $P(s, t)$ and $Z(s't)$ for weakly and more strongly unstable situations.

9 Advection

Another way to make the environment change periodically is to make the time derivative into an advective derivative, and to impose a flow that models ocean circulation. In the model that was simulated, the "ocean" is wind-driven, two layers with warm water above the thermocline and cold water below), and quasi-geostrophic. Figure 6 shows a snapshot of the mean s value from such a model with a single nutrient and a single predator. The diversity is highest in the region where the western boundary currents meet and proceed offshore as an eddying jet.
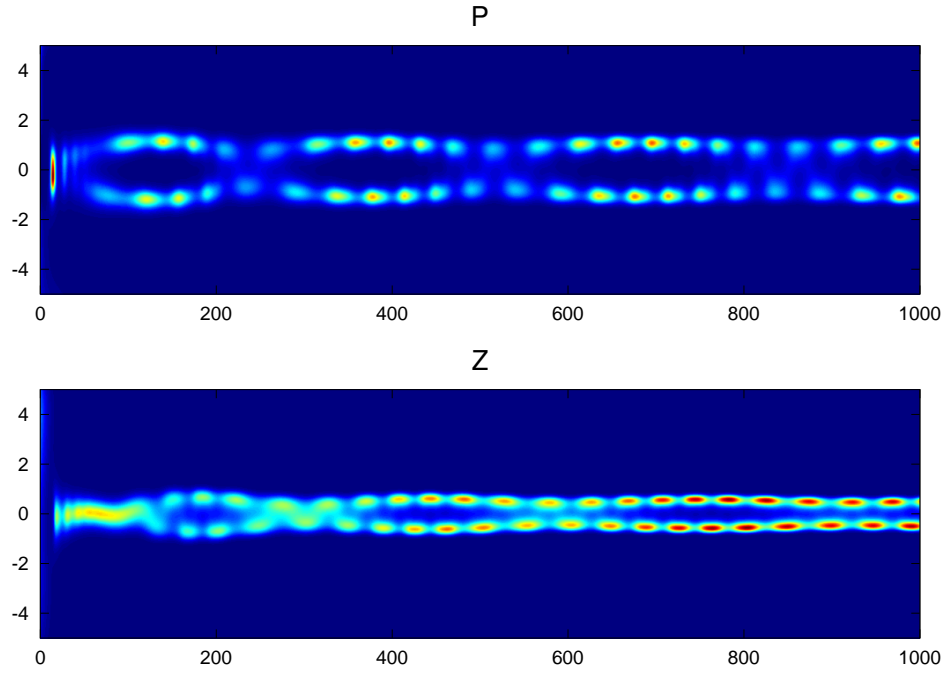
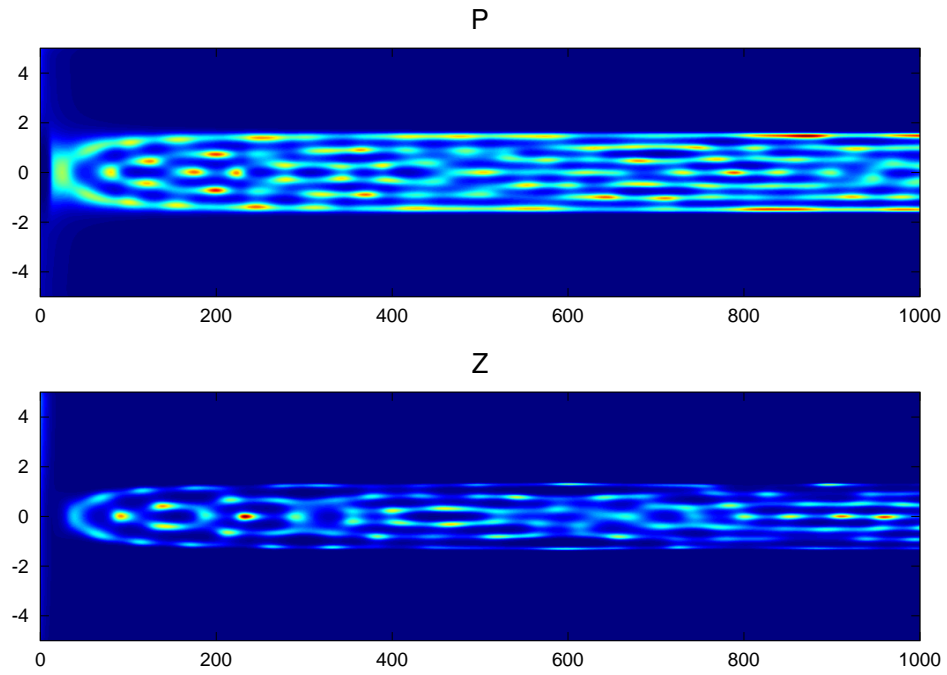Figure 4: Predator-prey biomass densities for $G''/G = 1.6\,\mu''/\mu$.

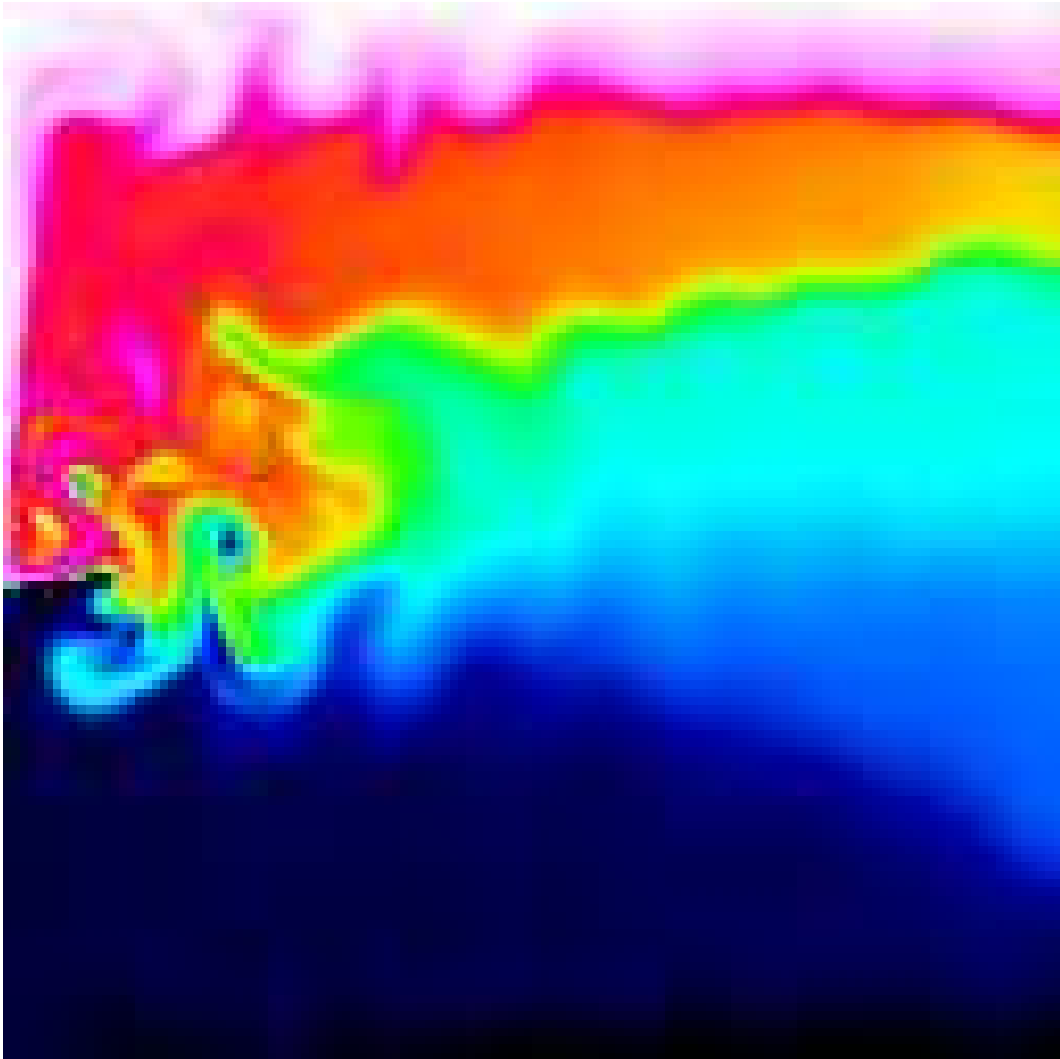Figure 5: Predator-prey biomass densities for $G''/G = 25\,\mu''/\mu$.

Figure 6: Mean value of s in a two-gyre, eddying model.